Activity Budget and Spatial Behavior of the Emerald Tree Boa *Corallus batesii*

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Abstract

Corallus batesii is a boid snake native to the Amazon basin. *C. batesii* was declared a distinct species from its sister species in 2009. Because of this recent taxonomic shift, much of the research on the basic biology and behavior of *C. batesii* and other *Corallus* boas has become muddled. This study serves to clarify their biology by analyzing the temporal, foraging, and spatial behavior of juvenile *C. batesii* in captivity at Zoo Atlanta. Hunting and movement behaviors were primarily nocturnal and resting behaviors were diurnal. Foraging strategy has yet to be analyzed. Qualitatively, site fidelity was observed in individual snakes with respect to both hunting and resting behaviors.

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Introduction

In recent years, there has been substantial clarification in the taxonomy within the *Corallus* genus, a widespread group of boas found in the Neotropics (Reynolds and Henderson 2018). Henderson et al. (2009) reviewed the widespread species known as the emerald tree boa (*C. caninus*) and recognized an additional species distinguished by range; while *C. caninus* occupies a range centered around the Guiana Shield region of South America, *C. batesii* is found in the Amazon basin (Henderson et al. 2009). Following the recent taxonomic distinction, it is now evident that there is a lack of basic research detailing the biology of several *Corallus* boas, particularly in behaviors that may make *C. batesii* ecologically distinct. This study aims to describe the behavior in juvenile *C. batesii,* in order to better understand their ecological role. To do this, we created an activity budget to record and measure behavior in regard to foraging, temporal, and spatial activities.

All species names used in this work have been adapted to their current classification (Reynolds and Henderson 2018). Notably, *C. enydris* (*sensu* Henderson 1993; Henderson and Winstel 1995) has been changed to reflect the current name *C. hortulanus* (*sensu* McDiarmid et al. 1996).

Snakes commonly exhibit one of two foraging behaviors: ambush predation or active foraging. While ambush predators sit and wait for their prey to come to them, active foragers move frequently in search of their prey (Huey and Pianka 1981). Among *Corallus* spp., both foraging methods have been reported (Yorks et al. 2003; Henderson 1993), and such diversity in foraging behavior could indicate phylogenetic, ontogenetic, or randomized individual differences (Huey and Pianka 1981).

Additionally, site fidelity—the tendency to return to the same area to carry out the same behaviors—can often be used as an indicator of foraging strategy, and it also implies the amount of space an organism requires to carry out essential activities. Because site fidelity is characterized by the snake's ability to return to the same spot, it also suggests a degree of cognition and memory. Furthermore, understanding foraging behavior and site selection provides insight into the ecological role of each of these snakes. Thus, our study is essential for the conservation and protection of their habitat.

Our research aims to fill gaps in understanding the behavioral biology of the *Corallus* species. While *C. batesii* has been researched in terms of biogeography and phylogenetic data, relatively little is known about their behavior (Henderson et al. 2009; Vidal et al. 2005). Like other arboreal snakes, *C. batesii* are difficult to study in natural environments due to their elevated position in dense forest habitats. Using six juvenile boas at Zoo Atlanta, we aimed to create an activity budget, which will map the behaviors of *C. batesii* (hunting, resting, movement, other) and record boa position in the enclosure for site-fidelity analyses.

Literature Review

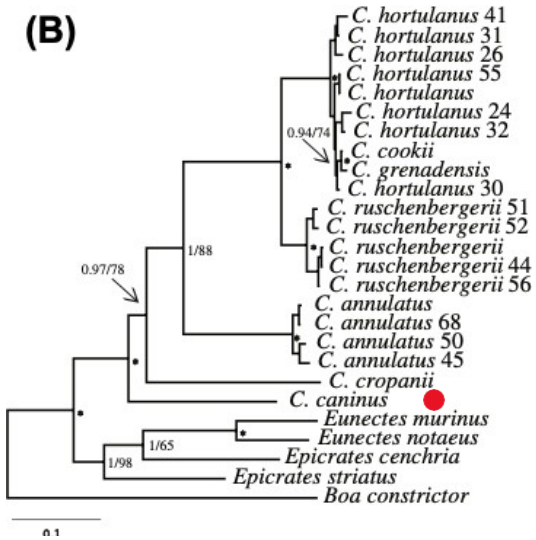

Figure 1. A partial phylogeny of *Corallus* adapted from Colston et al. (2013:fig1B). A genetic sampleof *C. batesii* was not available for phylogenetic analysis, but *C. batesii* is not currently questioned as a phylogenetic sister species to *C. caninus*, denoted with red dot (Henderson etal. 2009; Colston et al. 2013). Colston et al. (2013) recognized a need for further analysis, once a *C. batesii* sample is obtained.

Foraging Behavior

According to the foraging syndrome hypothesis, an organism's method of foraging—whether active or ambush-- is often a determined by a combination of behavioral, ecological, physiological and morphological characteristics (McLaughlin 1989; Beaupre and Montgomery 2007). Because active foragers encounter prey and feed more frequently, they have a more diverse diet (Anderson and Karasov 1981) and a greater risk of predation than do ambush predators (Beaupre and Montgomery 2007). Although there are two formally defined strategies, foraging type usually is fluid. It can vary across closely related species, within a species, and even within individuals during different life stages or feeding events (Beaupre and Montgomery 2007; Siers et al. 2018).

Table 1. A comparison of diet and foraging method in *Corallus* boas. Because of the diversity in diet and foraging method, further researcher is needed to understand the relationship between diet and foraging in *Corallus* spp.

Species	Diet	Foraging Method	Source
C. annulatus	Squirrels, bats, birds, & lizards	Ambush predators	Solórzano 2004
C. batesii	Mammals	Unknown	Henderson and Pauers 2012
C. blombergii	Unknown	Unknown	
C. caninus	Mammals	Unknown	Henderson and Pauers 2012
C. cookii	Reptiles, birds & mammals as adults	Unknown	Henderson and Pauers 2012
C. cropanii	Unknown	Unknown	
C. grenadensis	Juveniles: lizards Adults: mammals	Juveniles: active foragers Adults: ambush predators	Henderson and Pauers 2012; Yorks et al. 2003
C. hortulanus	Birds & mammals	Juveniles: active foragers Adults: ambush predators	Henderson 1993; Henderson and Pauers 2012
C. ruschenbergerii	Lizards, birds, small & large mammals	Unknown	Henderson and Pauers 2012; Solórzano 2004

Because the syndrome hypothesis connects behavioral and ecological characteristics, the target prey species and the diversity of prey may indicate a boa's feeding strategy. As seen in Table 1, both ambush and active foraging are documented among *C. hortulanus*, while foraging behavior in *C. batesii* is unknown. A phylogeny based on genetic data for *Corallus* was proposed by Colston et al. (2013; Fig. 1), and although a *C. batesii* sample was not included, from other morphological evidence, the authors believe *C. batesii* to be the sister species to *C. caninus* (Colston et al. 2013). A proposed phylogeny, that does not show the two species as sisters (Henderson 1993), discussed the evolution of diet in the *Corallus* clade, and stated that *C. batesii* feeds strictly on mammals. Later, however, Henderson (2012) expanded that notion to include predation on lizards by juvenile *C. batesii*. Consequently, further research is needed to clarify discrepancies in diet and behavior.

In *C. grenadensis*, Yorks et al. (2003) determined that smaller, and therefore younger, *C. grenadensis* move more frequently and for longer periods of time, classifying them as active foragers, but the larger boas were not classified into a foraging category. However, in *C. hortulanus*, distinctive ontogenetic stages are evident. Boas <60 cm in length primarily ate *Anolis carolinensis*, foraged 1–4m above the ground, and were considered active foragers. Boas >110 cm in length primarily ate endotherms, such as rodents, foraged below 1m, and were considered ambush predators (Henderson 1993). While there are substantial data on the diets of the *Corallus* boas, it is not understood how they forage. Clarifying the foraging behaviors of *Corallus* boas will allow us to better understand the relationship between ontogenetic stage, diet, and foraging mode. Furthermore, understanding this relationship is critical to developing conservation practices for these boas in the natural environment and in captivity.

Temporal Behavior

In addition to documenting foraging style, we created an activity budget to analyze *C. batesii* behavior for temporal differentiation. We assessed whether behavior is demonstrated at a specific time daily and whether the behavior varies significantly throughout the year (Altmann 1974; Martin and Bateson 1993). In natural situations, snakes are difficult to monitor over long periods of time, and arboreal snakes provide an additional challenge because they can be difficult to view. Additionally, because snakes don't live in social groups, only one snake's behavior can be analyzed at a time. Therefore, in the wild, focal sampling is often required to closely track individuals for later comparison. Because we filmed *C. batesii* at Zoo Atlanta, we were able to monitor the snakes continuously for a more comprehensive analysis.

Among the previously studied *Corallus* spp., only *C. hortulanus* has a documented activity budget. After a feeding event, researchers were able to monitor behavior in response to the hour of day (Henderson and Winstel 1992). Ninety percent of *C. hortulanus* foraging behaviors were documented between the hours of 1800–2400 (Henderson and Winstel 1992). *C. hortulanus* rested on exposed branches between the hours of 2400–0502, and they retreated into the leafy interior between the hours of 0540–0900 (Henderson and Winstel 1992), and they hypothesized that these time constraints are a way for the ectothermic boa to conserve body heat during the coolest period of the night (Henderson and Winstel 1992). The active hours begin at dusk and dawn, which suggest that visual and/or thermal cues drive *C. hortulanus* behavior. While *C. hortulanus* are considered active foragers as juveniles, they shifted to an ambush predation style as adults (Table 1).

In contrast, a consistent ambush predation strategy was found in *Crotalus horridus* (Timber rattlesnake, a distantly related species to *Corallus* boas). Field researchers recorded instantaneous behavior for 3 years and found hunting behavior between hours of 2100–0800, with an average hunting time of 7 hours per night (Reinert et al. 1984). Although it is likely that the foraging strategy of *Corallus batesii* most resembles its closer relative, *C. hortulanus*, Reinert et al. (1984) will serve as a comparison for determining predation style.

Spatial Behavior

Finally, we analyzed the spatial behavior exhibited in *C. batesii*. Learned site fidelity likely exists because of reward assurance. Success is defined as completing a behavioral activity, which could include a successful predation event or undisturbed resting, and a repeatedly successful behavior encourages an organism to return to the same area, whereas repeated failure encourages an organism to move to a new location (Switzer 1993). Unpredictable environments make it difficult to determine success versus failure, but using models, it was determined that even partially secured success encourages learned site fidelity across vertebrate taxa (Switzer 1993).

In snakes, site fidelity in hunting would be strong in individuals that utilize an ambush predation strategy because they must find a spot to consistently obtain prey (Reinert et al. 1984). Individual site fidelity has not been analyzed before with respect to spatial coordinates, but in *Gloydius shedaoensis*, a pit viper, researchers looked at site fidelity with respect to environment (Shine and Li-Xin 2002). All ambush vipers studied had strong nonrandom site selection with respect to

the species of tree, isolated trees vs. tree in a thicket, prey abundance, branch diameter, and branch orientation (Shine and Li-Xin 2002).

Corallus hortulanus is the only *Corallus* boa that has been analyzed for habitat selection, and individual site fidelity has not been monitored in any *Corallus* spp.. Although individual site selection was not analyzed in *C. hortulanus*, researchers found that smaller boas spend the majority of their time in uncultivated woods, while larger boas spend more time in mango and other cultivated trees (Henderson and Winstel 1995). Due to ontogenetic differences in diet, Henderson and Winstel (1995) hypothesized habitat selection in *C. hortulanus* to be differentiated based on size class.

Because Zoo Atlanta had juvenile *C. batesii* in captivity, we had a unique opportunity to monitor their behavior continuously. Since these boas are fed on regular intervals and were quite young, it is unlikely that there is learned site fidelity due to hunting in the environment. However, if site fidelity is present, it evidences that some aspects of their site fidelity may actually be attributed to instinctual preference for certain environmental conditions, such as branch diameter or perch height, rather than a purely learned behavior.

Methods

Overview

Five juvenile *C. batesii* (5 mo. at beginning of study) were kept in enclosures in a room isolated from public viewing at Zoo Atlanta (*Fig. 2*). The study includes both male and female juvenile boas from the same litter (3M, 2F). Snakes were fed once every 26–27 days. The time between meals is established as a feeding period. Each *C. batesii* was video recorded over two feeding periods (beginning on 23 July 2019 and 18 August 2019). For each snake, we collected data on the third hour every other day for 45 minutes. These sampling periods were designed to produce a data set of manageable size and to ensure data for both diurnal and nocturnal periods.

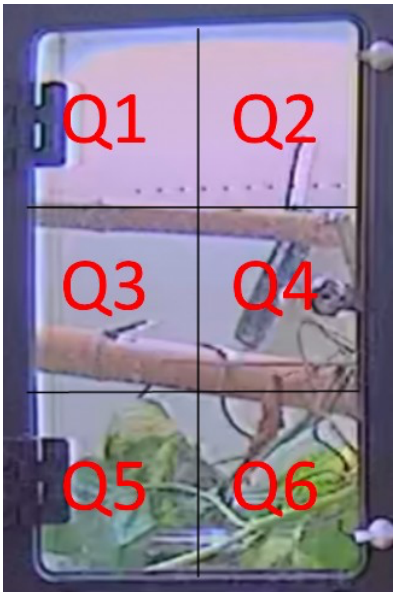

Figure 2. Representative study enclosure for *C. batesii* at Zoo Atlanta. Two-dimensional spatial grid is shown as it was used for site fidelity analyses (see Methods).

Foraging and Temporal Behavior

Our ethogram was initially defined from behaviors previously described in *Crotalus horridus* (Reinert et al. 2011: fig. 4) and was modified based on initial observations of *C. batesii*. Our modified ethogram for *C. batesii* included both stationary (hunting, resting, other) and active behaviors (movement, other). Out-of-view was used when the boa was not visible in its enclosure (Table 2). We collected data using Boris (Friard and Gamba 2016) software, and inter-observer reliability tests were required prior to behavioral recordings. From this data collection, we assessed foraging strategies and daily activities with both continuous and instantaneous recordings for a comprehensive behavioral analysis.

Table 2. *Corallus batesii* Behavioral Ethogram.

Stationary Behaviors • Stationary position for a minimum of 5 seconds			**Active Behaviors**		**Out of View**
Hunting	Resting	Other (Stationary)	Movement	Other (active)	
Three-point S-curve in neck **AND** Head not resting on body	In clasping coil **AND** Not in hunting posture	Not in hunting or resting posture **OR** Stationary, but head not visible	Head extend away from body **OR** Entire body in motion	Partial motion **AND** Back of body not visible	Not visible

Because we are interested in the progression and duration of each snake's behavior (hunting, resting, movement, other), we used continuous sampling to measure the amount of time boas exhibited each behavior within the 45-minute sampling period, and we used the frequency of occurrences to record the switches between any two defined behavioral activities. The duration informed if activities were performed at certain times of day or within certain times in a feeding period, whereas occurrences demonstrated whether the boas exhibit active foraging (i.e., many occurrences of hunting and movement within the hour) or ambush predation (i.e., few instances of hunting or movement; one or two positions within the hour).

In order to assess differences in behavior for time of day, videos were grouped into diurnal and nocturnal periods based on the enclosure light (enclosure light on: 0900–1700hr; enclosure light off: 1800–0800hr). Because this data was not normally distributed (Kolmorgorav-Smirnov test, p= 2.2e-16), a Mann-Whitney U test was used to assess differences for each behavior during diurnal and nocturnal periods.

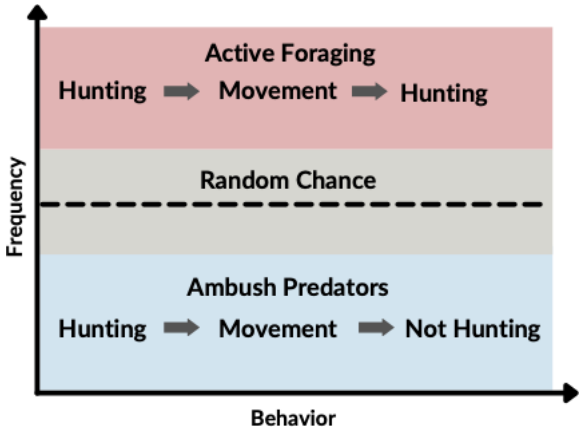

Figure 3. The order of recorded events used to determine predation style. Active foraging (red) indicates more frequent switches between hunting to movement to hunting. Ambush predation (blue) indicates low frequency in switches, and switches from hunting to movement to a behavior other than hunting.

To assess foraging mode, all recorded hours where at least one instance of hunting were analyzed. For each of these videos, the order of behaviors was tracked for the 45-minute recording. Foraging mode—ambush predation or active foraging-- was determined by frequency of behavioral switches (Fig. 3). Active foragers switch between hunting to movement and back to hunting significantly more than hunting to movement to any other behavior. Ambush predators will have low frequency of behavioral switches because long-duration hunting bouts will be the predominant behavior.

Spatial Behavior

To assess site fidelity, we used ZooMonitor (Ross et al. 2016) mapping software. When a boa exhibited stationary (hunting and resting) positions, the location was recorded on a 2D map of the enclosure (Fig 2). Using the ZooMonitor software, heat maps were generated to qualitatively assess preferential location when hunting and resting positions were observed. The 2D enclosure was then segmented into six equivalent sections (Fig. 2), and site fidelity was confirmed using a Kruskal-Wallis and Wilcoxon rank test to determine if a boa spent significantly more time within any one quadrant. Individual enclosures were furnished with different orientations, so the presence and absence of location preference was compared between boas, rather than the relative position within each enclosure.

Site fidelity was analyzed using a T-test to compare presence and absence between boas for both resting and hunting positions.

Results

Hunting and movement were both found to predominantly occur during the nocturnal (lights off) hours, while resting was found to occur during the diurnal (lights on) hours (Fig. 4). Few individual differences in behavior duration were found for each snake, but the majority of the snakes exhibited significantly similar behaviors (Fig. 5). Little variation between individual snakes indicate the species as a whole behaves similarly.

Foraging style has not yet been analyzed.

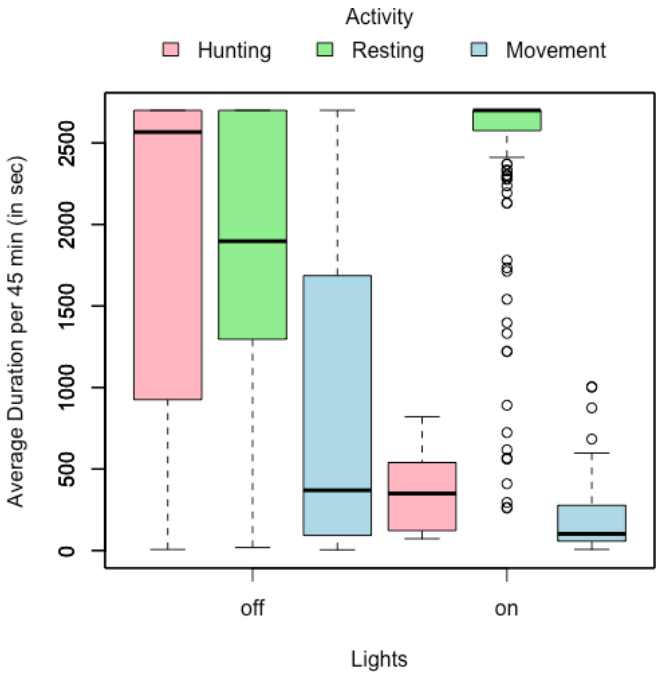

Figure 4. Average duration in a behavior: hunting (pink), movement (blue), resting (green) comparing lights on and lights off. Hunting and movement occurred significantly longer when the enclosure light was off and resting occurred significantly more when the light was on. Hunting (W = 662, p-value = 0.004519), Resting (W = 1865.5, p-value = 1.871e-05),

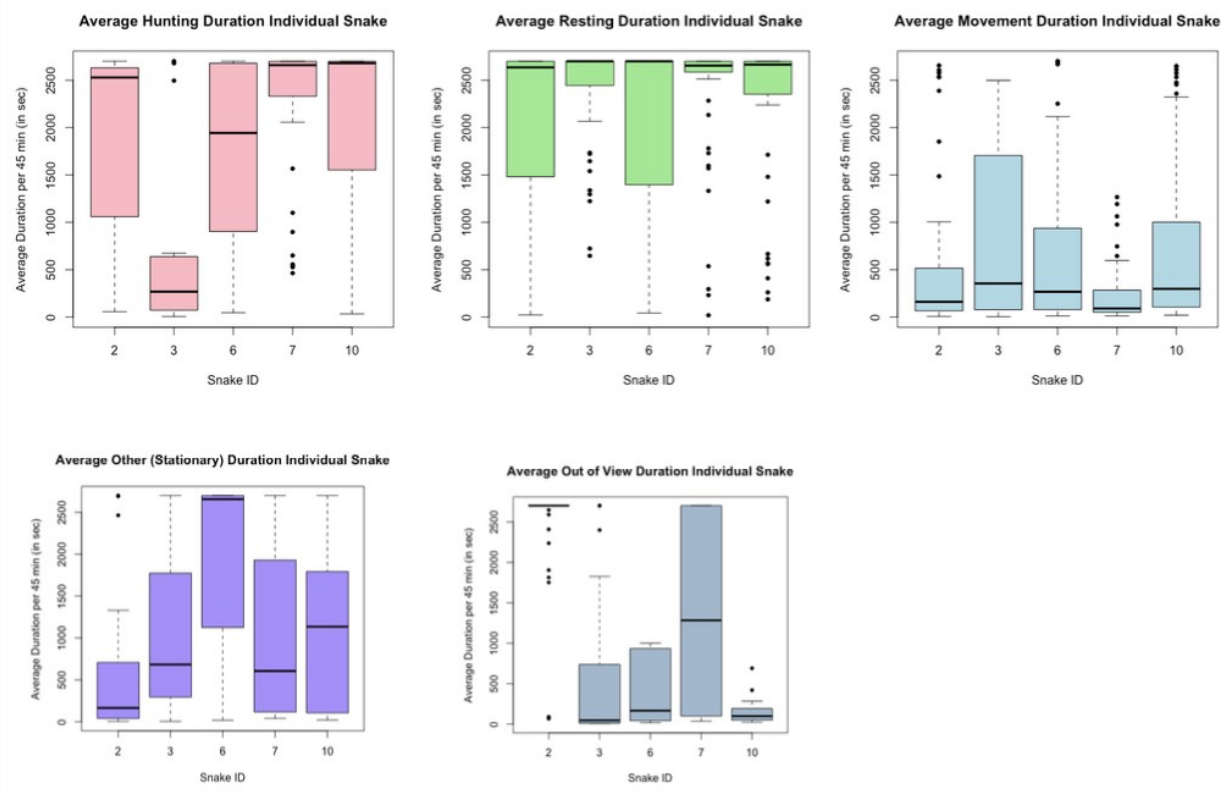

Figure 5. Individual variation in behavior length for each snake ID. No significant difference was detected in resting behavior (Kruskal-Wallis chi-squared = 4.1861, df = 4, p-value = 0.3814). Differences in hunting behavior (Kruskal-Wallis chi-squared = 29.433, df = 4, p-value = 6.383e-06) were found between Snake 3 and all other snakes. Differences in movement (Kruskal-Wallis chi-squared = 14.64, df = 4, p-value = 0.00551) were evident between Snake 7 with snakes 2, 3, 6. Differences in other stationary (Kruskal-Wallis chi-squared = 41.689, df = 4, p-value = 1.935e-08) were detected between Snake 6 and all other snakes and between Snake 2 and Snake 10. Differences in out-of-view (Kruskal-Wallis chi-squared = 62.129, df = 4, p-value = 1.035e-12) were evident between Snake 2 and snakes 3, 6, 10 and between snake 7 and 3, 6, 10.

Site fidelity has only been analyzed qualitatively, but it appears that snakes exhibit strong site fidelity while resting and weak or no site fidelity while hunting (Fig.6).

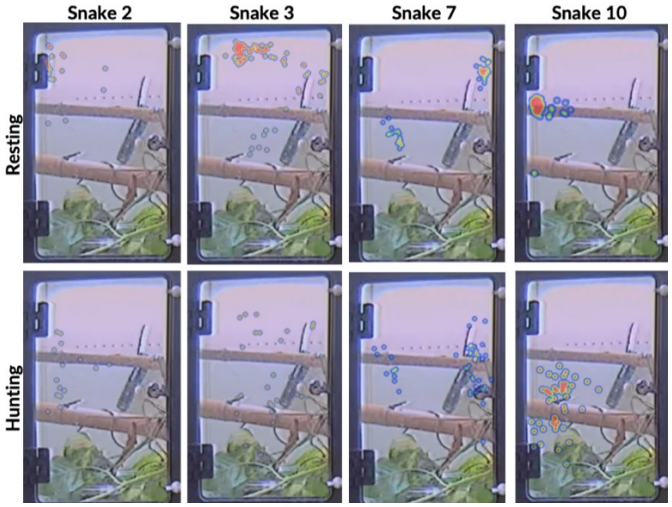

Figure 6. Site fidelity heat maps for individual snakes. Qualitatively, resting (top) has dense cluster groups, indicating stronger site fidelity than hunting (bottom).

Discussion

In *C. batesii*, hunting and movement behaviors were primarily observed when the enclosure light was off (Fig. 4). Since hunting occurs during dark hours, this suggests that *C. batesii* are primarily nocturnal foragers, similar to other boid species (Pizzatto et al. 2009). Boas utilize labial pit organs to detect infrared radiation in endothermic prey, and because of this, endothermic prey is typically hunted at night (Amemiya et al. 1999).

Although there are few studies in other *Corallus* spp., the existing literature suggests that *C. caninus* primarily consume mammals, while *C. hortulanus* undergo an ontogenetic shift in diet from anura and lizards as juveniles to a mammalian diet as adults (Pizzatto et al. 2009; Henderson and Pauers 2012). In *Crotalus horridus*—and other pit vipers—ambush foraging is common, but little to no variation exists between size classes (Reinert et al. 1984). Pit vipers have a more effective pit organ for sensing infrared radiation in endothermic prey than boas (Amemiya et al. 1999). The ontogenetic shift to a mammalian diet that occurs in *C. hortulanus* could signify stronger development of their pit organ with age, making them more effective ambush predators when they are larger in size.

Forging style has not yet been analyzed. Because *C. caninus*, the sister species of *C. batesii*, is documented to forage only on mammals without an ontogenetic change in diet, they are likely ambush predators. If we find that *C. batesii* are also ambush predators, we can conclude that *C. caninus* and *C. batesii* have diverged in foraging style from *C. hortulanus*. However, if we find that our study of juvenile *C. batesii* are active foragers, this may imply that they also undergo an ontogenetic shift in diet and foraging style. In this situation, we will need to further assess the foraging style in other *Corallus* spp. to understand how foraging method evolved in this genus.

Because this study was performed in captivity, we had the ability to observe fine-scale and individual site selection otherwise not possible in natural in arboreal boas in natural rainforest canopies. As previously described, site selection in some snakes primarily is characterized based on ontogenetic class due to differing diets (Henderson and Winstel 1995; Shine and Li-Xin 2002). Our results qualitatively demonstrate that there is site fidelity with respect to resting in all analyzed boas (Fig. 6), which may indicate that *C. batesii* prefer certain environmental conditions for resting like perch height, branch diameter, and leaf coverage. Qualitatively, *C. batesii* does not have site fidelity during hunting and does not exhibit similar resting preferences.

As the first type of spatial analysis of this kind in *Corallus* spp., we will need future research to discern if these behaviors are present in wild populations. Additionally, the presence of site fidelity will drastically improve population surveys for *C. batesii* and other boas as researchers will have more information about where to look for these species.

Conclusion

This study serves as a starting point for understanding the behavioral nuances of *C. batesii*. Their behaviors are temporally associated, and they show preferences in spatial locations. In addition to these results, further research will be needed to compare the other *Corallus* boas. When methodology and resources are available, *C. batesii* behavior should be documented under

natural conditions and compared with our study in captivity, so we can conserve *C. batesii* in natural environments and provide adequate care in captive programs.

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